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NABICULA (*LIMNONABIS*) *PROPINQUA* (REUTER) (HETEROPTERA: NABIDAE): DIMORPHISM, PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY

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The taxonomy and distribution of the North American species *Nabicula propinqua* (Reuter), is reviewed. The macropterous form occurs in both sexes, but is much less common than the brachypterous form. Macropterous forms of both sexes have wider pronota. Males have disproportionately longer antennae than females. Male and female genitalia of *N. propinqua* are described and illustrated. The genitalia of individuals from isolated west coast populations differ only slightly from those of eastern populations. A cladistic analysis of the subgenus *Limnonabis* Kerzhner is presented and a new species-group classification suggested. A biogeographic hypothesis explaining the present distribution of *Limnonabis* is presented. We suggest that *N. propinqua* is a vicariant species that was isolated from a population contiguous with that in western Europe with the opening of the Atlantic Ocean.

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Introduction

Nabicula (*Limnonabis*) *propinqua* (Reuter), recognized by its large size and elongate, slender form, is one of the most conspicuous North American species of Nabidae (fig. 1). Unlike some of the commonly encountered species of *Nabis* that occur on vegetation in a variety of habitats, *N. propinqua* is rare in collections and lives on the ground or low vegetation in marshy habitats (Blatchley 1926). In addition to *N. propinqua*, five other species in the genus *Nabicula* Kirby occur in North America (Henry & Lattin 1988). *N. propinqua*, however, is the only member of the subgenus *Limnonabis* Kerzhner in North America, the other five species occur in Europe and Eastern Asia.

The most recent nomenclature (Kerzhner 1988) considers *Nabicula* a subgenus of *Nabis*, and does not recognize *Limnonabis* as a taxonomic group. In this paper, however, we use the nomenclature of Kerzhner (1981) because this classification has also been used in recent faunistic works for Europe (Péricart 1987) and North America (Henry & Lattin 1988). In addition, species relationships within *Nabicula* are still unresolved and we anticipate the nomenclature of Kerzhner (1988) to change again (unpublished data).

Reuter (1872) described *N. propinqua* in *Nabis* Latreille from a single brachypterous female specimen from Wisconsin, and described *vicarius* (in *Nabis*) from a single brachypterous male from Illinois. Reuter (1880) synonymized *vicarius* with *propinqua*. Hart (1907) described *elongatus* (in *Nabis*) from a single macropterous male from Havana, Illinois. This species was synonymized with *propinqua* by Van Duzee (1916).

In this paper, we summarize the distribution and habits of *N. propinqua* and describe the internal genitalia for both the male and female. We also present a cladistic analysis of the subgenus *Limnonabis* and provide a hypothesis of the biogeographic history of the taxon.

Descriptive part

Distribution

Nabicula propinqua occurs along the eastern seaboard from Maryland to Maine and extends westward between 40 and 50 degrees N latitude throughout the Great Lakes region to North Dakota (fig. 2). West of the 100th meridian, *N. propinqua* occurs much farther north, with records

from Alberta, Manitoba, Quebec and above 60 degrees N latitude along Great Slave Lake in the Northwest Territory. Essentially the distribution of *N. propinqua* follows the Saline Lakes and Forest Zone of Freshwater Lakes limnological regions of Northcate & Larkin (1966). There are at least two populations of *N. propinqua* that are disjunct from the main distribution. We have collected *N. propinqua* from two localities in the coastal marshes in Oregon and have examined a single specimen from Meade Co., Kansas.

With the exception of the latter three records, most of the known distribution of *N. propinqua* occurs within the area occupied by the ice sheet of the Wisconsin Glaciation. If *N. propinqua* was present in North America during the Pleistocene, as we will argue, it must have been restricted to areas south of the ice sheet or in one of the far northern refugia (Matthews 1979). Because *N. propinqua* is not yet known to occur in the areas of northern glacial refugia, it seems likely that *N. propinqua* moved into the areas it now occupies from areas south of the Wisconsin ice sheet sometime within the last 10,000 years. In this scenario, the Kansas specimen probably represents a Pleistocene relictual population in an area previously occupied by *N. propinqua*. Other such populations are likely to be located (e.g. the marshes in the Sand Hills of western Nebraska).

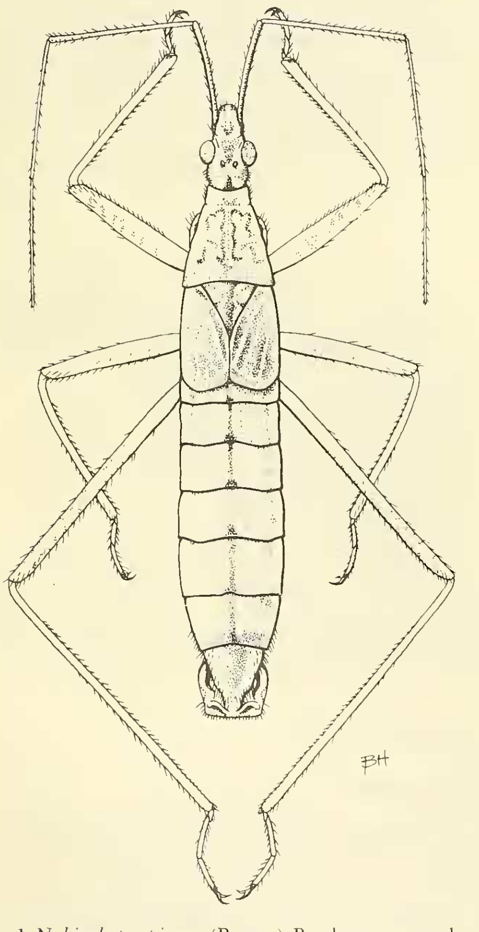


Fig. 1. *Nabicula propinqua* (Reuter). Brachypterous male. Dorsal habitus.

The origin of the Oregon coast population is more perplexing. *N. propinqua* has not yet been found in the arid Inter-mountain region, nor in the mesic Willamette Valley and Puget Trough areas of Oregon and Washington. It appears to be restricted to the coastal marshes of Oregon and possibly Washington. Lattin (1966) suggested that this population might be an introduction from the eastern United States. Now, however, we believe this unlikely, considering the restricted habitat of this species and the fact that the Oregon population displays a slightly different genitalic structure than eastern populations (see below).

If *N. propinqua* or its direct ancestor was present in North America by the Eocene as we hypothesize (see Discussion), there were few barriers to impede East-West movement and a contiguous distribution across the northern latitudes would have been possible. Beginning in the Miocene, orogenic activity in western North America resulted in topographical geographic barriers and, perhaps more importantly, increased aridity in the Intermountain region. Because *N. propinqua* lives in moist, riparian habitats, this dramatic change in climate and terrain would have restricted mobility and could have led to the extinction of many, or all of the intervening populations.

This is merely a hypothesis of course, and we cannot actually date the separation of the west coast population and it is possible that it is a much more recent event. The climate of the northern United States during the Pleistocene periods was much more mesic than the present, with abundant, large shallow lakes and marshes throughout the Great Basin province (Smith 1978). This would have provided abundant habitats for *N. propinqua* from the Rocky Mountains west. With the advent of the Hypsithermal and higher temperatures, these habitats in this area largely disappeared (Barnosky et al. 1987), which could have left the coastal population isolated from those north and east of the Rockies. This hypothesis would be corroborated if relictual populations of *N. propinqua* were found in isolated marshes in the northern Great Basin.

Dimorphism

In many nabids, males and females often differ markedly in size, occurrence of wings and propor-



Fig. 2. Distribution of *N. propinqua* in North America. Circles represent specimens examined, triangles are literature records only. Solid line indicates maximum extent of Wisconsin ice sheet.

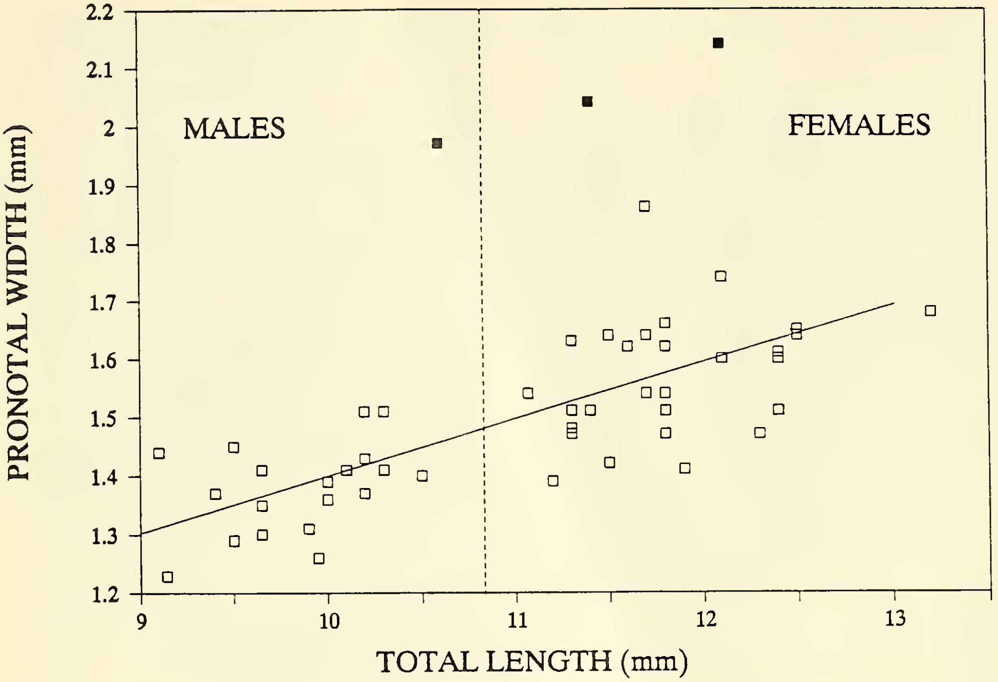


Fig. 3. Relationship between the posterior width of the pronotum and total length in *N. propinqua*. $y = 0.093239(x) + 0.465369$, $r^2 = 0.565$. Open squares are brachypterous specimens. Solid squares are macropterous specimens.

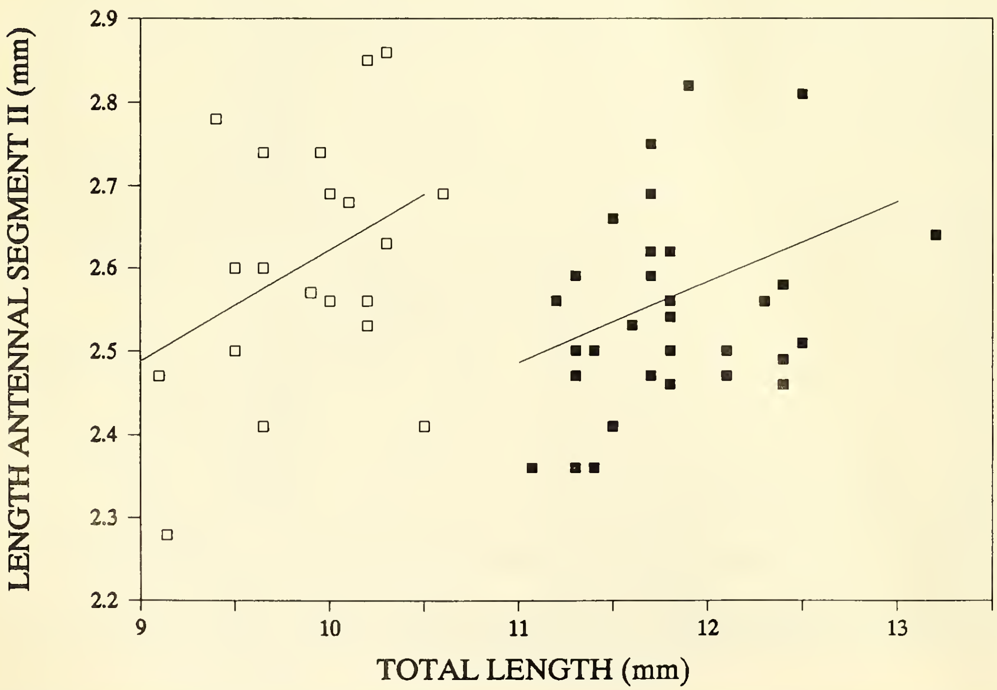


Fig. 4. Relationship between the length of the second antennal segment and total length in *N. propinqua*. Open squares are males. $y = 0.13069(x) + 1.318405$, $r^2 = 0.149$. Solid squares are females. $y = 0.077957(x) + 1.62609$, $r^2 = 0.101$.

Table 1. Comparison of six measurements among brachypterous and macropterous male and female *Nabicula propinqua*. Data are mean and (range) in mm.

	TL	VERT	PPW	PL	A1	A2
male	9.8	0.405	1.39	1.53	1.66	2.60
	(9.1-10.6)	(0.38-0.44)	(1.23-1.51)	(1.41-1.69)	(1.51-1.85)	(2.28-2.86)
Brach M	10.5	0.41	1.97	1.69	1.70	2.69
female	11.8	0.444	1.57	1.73	1.65	2.55
	(11.0-13.2)	(0.39-0.48)	(1.39-1.86)	(1.61-1.86)	(1.53-1.85)	(2.36-2.82)
Brach F	11.8	0.41	2.09	1.86	1.60	2.49
	(10.3-12.1)	(0.40-0.42)	(2.04-2.14)	(1.83-1.89)	(1.59-1.60)	(2.48-2.50)

tions of body parts, but rarely are these differences quantified. We examined sexual dimorphism in six measurements, total length (TL), length of antennal segment one (A1), length of antennal segment two (A2), width of the vertex (VERT), posterior pronotal width (PPW) and pronotal length (PL). Measurements using an ocular micrometer were made of 21 males and 32 females from throughout the range of *N. propinqua*. We found differences between sexes in four of the six measurements. TL, VERT, PPW and PL, were greater in females than in males, but there were no differences between males and females for A1 and A2 (table 1). The differences between sexes seen in the former characters are explained by the positive linear relationship between these characters and the absolute size of the individual. For example, PPW increases with TL, and because females achieve a greater TL than males, they also display a greater PPW (fig. 3). We do not consider these characters true sexual dimorphisms therefore, but only size dependent characters.

The lengths of antennal segments also displayed an increase with TL, but only within a given sex. This is demonstrated by the fact that the slopes of the A2-TL regressions for the two sexes are the same ($F = 0.415$, $P = 0.523$), but the Y intercepts are different ($F = 8.662$, $P = 0.005$) (fig. 4). This indicates that although females are larger than males (greater TL), small males have the same length antennae as small females and large males have the same length antennae as large females.

Thus, in males, the antennae are disproportionately longer than in females. The length of the antennae seems to be uncoupled from the general correlation with body size that other measurements show. This relationship does not appear to be common in the Nabidae. In a preliminary analysis of four species of *Nabis*, males did not have disproportionately longer antennae, but rather there was a linear relationship between antennal length and size across the sexes.

Macroptery

Nabicula propinqua usually occurs in the brachypterous state, with the apex of the fore wings reaching to the middle of the second abdominal tergite (fig. 1). Macropterous females have been reported by Harris (1928) and Froeschner (1971). Only 2 of 45 females we examined were macropterous. In these individuals, the fore wings reached the middle of the seventh abdominal tergite. The hind wings are equally well developed, reaching to the anterior margin of the seventh abdominal tergite (fig. 5a).

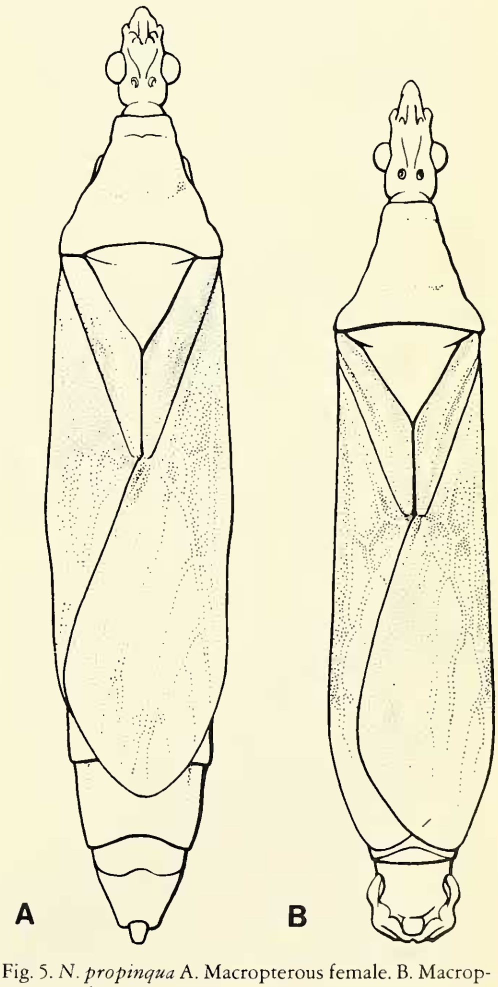


Fig. 5. *N. propinqua* A. Macropterous female. B. Macropterous male.

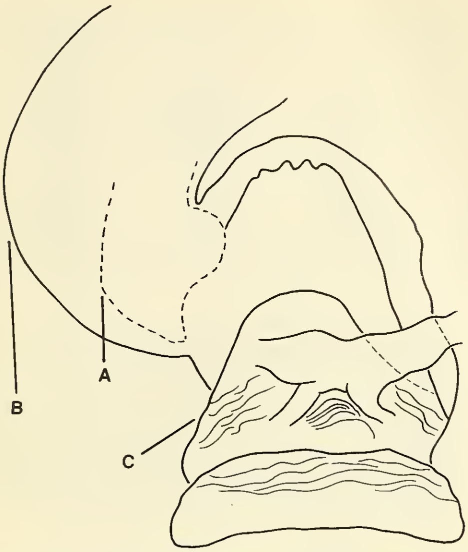


Fig. 6. Seminal depository of female *N. propinqua*. Dorsal view. A. Sclerotized ring. B. Membranous sac. C. Muscular lobe ventral to oviducts.

We have examined 29 male specimens and have seen only one macropterous individual (fig. 5b). This specimen was the holotype of *Nabis elongatus* Hart and is deposited in the Illinois Natural History Survey collection (INHS). Although Harris examined the material in the INHS (we have seen specimens with his determinations), he apparently overlooked this specimen, because he stated (Harris 1928) that males may never occur in the macropterous state. In England and on the Continent, only the females of *Nabicula lineata* (Dahlbom) are known in the macropterous form (Southwood and Leston 1959). Macropterous females and males have been reported for *N. ussuriensis* (Kerzhner) in eastern Asia (Kerzhner 1968).

Differences in the structure of the pronotum between brachypterous and macropterous specimens have been reported for both the latter two species. In *N. lineata*, the pronota of brachypterous specimens are 1.1 times as long as wide and in the macropterous forms the length and width are equal (Péricart 1987). In *N. ussuriensis*, the pronotum in brachypterous specimens is 1.1-1.2 times as long as wide and only 0.94 times as long as wide in macropterous specimens (Kerzhner 1968).

In *N. propinqua*, the ratio of PL to PPW is lower in the macropterous form (0.85-0.89) than the brachypterous form (1.05-1.15) in both males and females. The lower ratio results not from a shortening of the pronotum in the macropterous form, but from an increase in the width (fig. 3). In particular, the posterior lobe of the pronotum is greatly flared. The increased width of the pronotum is probably an indirect effect of the development of flight muscles and phragmata in the pterothorax of the winged form (Darnhoffer-Demar 1969). Because the anterior end of the mesothorax is enclosed by the posterolateral angles of the pronotum, an increase in diameter of the mesothorax would cause a similar change in the posterior lobe of the pronotum.

Female Genitalia

The seminal depository is large and dome-shaped, consisting of a fleshy external portion and a partially sclerotized internal structure, the apex of which bears three to five blunt sclerotized teeth (fig. 6). A thick muscular structure lies between the base of the depository and the oviduct. The sclerotized ring is a single structure occupying the ventral surface of the left side of the depository, extending from the depository laterally and curving anteriorly. It is surrounded by a large membrane also directed anteriorly.

Male Genitalia

Parameres

Reuter (1872) and Harris (1928) provided lateral views of the left paramere of *Nabicula propinqua*. Paramere morphology in some groups of Nabidae is very conservative (e.g. the genus *Nabis*) and *N. propinqua* displays this general form (fig. 7). Within the subgenus *Limnonabis*, the paramere of *N. propinqua* most closely resembles that of *N. pontica*. In contrast, *N. lineata* displays an unusually elongate apex. In some specimens of *N. propinqua*, the apex of the paramere is slightly bent laterally, a condition which is strongly developed in *N. ussuriensis* (Kerzhner) and *N. demisa* (Kerzhner 1968, 1981).

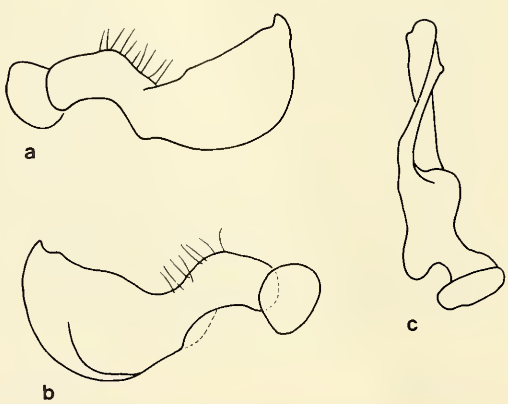


Fig. 7. Right paramere of *N. propinqua* A. Lateral view B. Medial view. C. Ventral view.

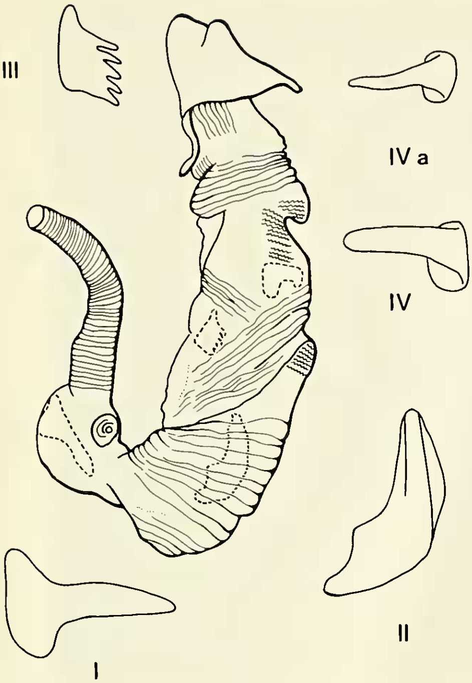


Fig. 8. Male aedeagus of *N. propinqua* from Oregon. Sclerites indicated by roman numerals. IVa. sclerite IV of specimen from Illinois.

Aedeagus

The aedeagus of *Nabicula propinqua* is very similar to that of *N. lineata* and *N. pontica.* The membranous portion of the aedeagus has four sclerites (fig. 8). No nomenclature has been proposed for the aedeagal sclerites of the Nabidae, and here we number the sclerites with Roman numerals beginning at the base of the aedeagus (sclerite I) and moving to the apex (sclerite IV). Sclerite I is linear and parallel to the longitudinal axis of aedeagus; it has a wide base and slightly tapering distal arm with a blunt, rounded apex. Some specimens may display a slight flange on this sclerite. Sclerite II is pistol-shaped, with a wide, arcuate base, a curved obtuse angle near its midpoint and a tapering, rounded distal arm. The distal arm bears flanges on both edges reaching from angle to apex. Sclerite III is roughly quadrangular and distinctly comb-shaped, with five short, blunt teeth directed toward the midline of the aedeagus. Sclerite IV is situated transversely in the aedeagus, with a broad, oval base. This sclerite exhibits geographic variation. In specimens from the Oregon coast, the sclerite has a thick, bluntly rounded arm (fig. 8 IV), and in specimens from east of the Rocky Mountains, the arm is longer, thinner, with a more pointed apex. (Fig. 8 IVa). There are two areas with sclerotized denticles along the folds of the membrane, one area distal to sclerite II and the other distal to sclerite IV. These denticulate areas are also present in identical form in related species.

PHYLOGENETIC ANALYSIS

To understand the origin and evolution of *Nabicula propinqua* in North America, it is necessary to identify its phylogenetic relationship to other taxa. Within *Nabicula*, Kerzhner (1981) recognized three subgenera, *Limnonabis* Kerzhner, *Dolichonabis* Reuter, and *Nabicula* Kirby. He distinguished the subgenus *Limnonabis* from *Dolichonabis* (sensu strictu) by the diverging posterior lobe of the head, recurved connexivum of the male and the presence of three or four sclerites in the aedeagus. Within *Limnonabis*, he identified two groups, the *lineata* group composed of *N. lineata*, *N. pontica* and *N. propinqua*, identified by the large parameres and multiple rows of spines of Ekblom's organ (see fig. 11). The *ussuriensis* group contains *N. ussuriensis* (Kerzhner), *N. demisa* (Kerzhner) and *N. sauteri* (Poppius), united by the small parameres and the single row of spines (see fig. 10).

To further clarify the relationships among these taxa, we conducted a cladistic analysis of the subgenus *Limnonabis* using the computer program HENNIG 86 (Farris 1988). Because we were not able to examine specimens of all species in the subgenus, we used characters that were described and/or illustrated for the other taxa by Kerzhner (1968, 1981) and Péricart (1987). We used structures of the male

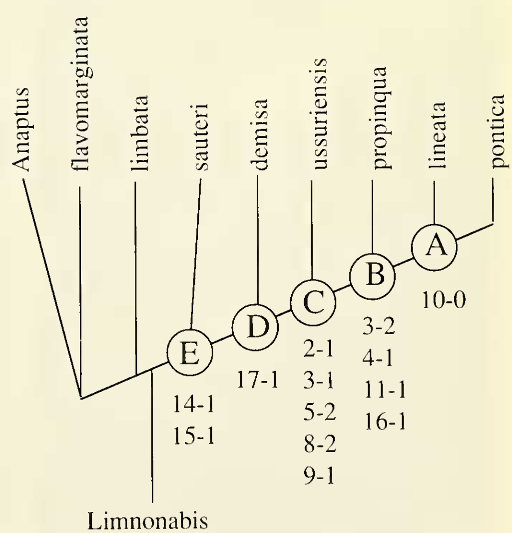
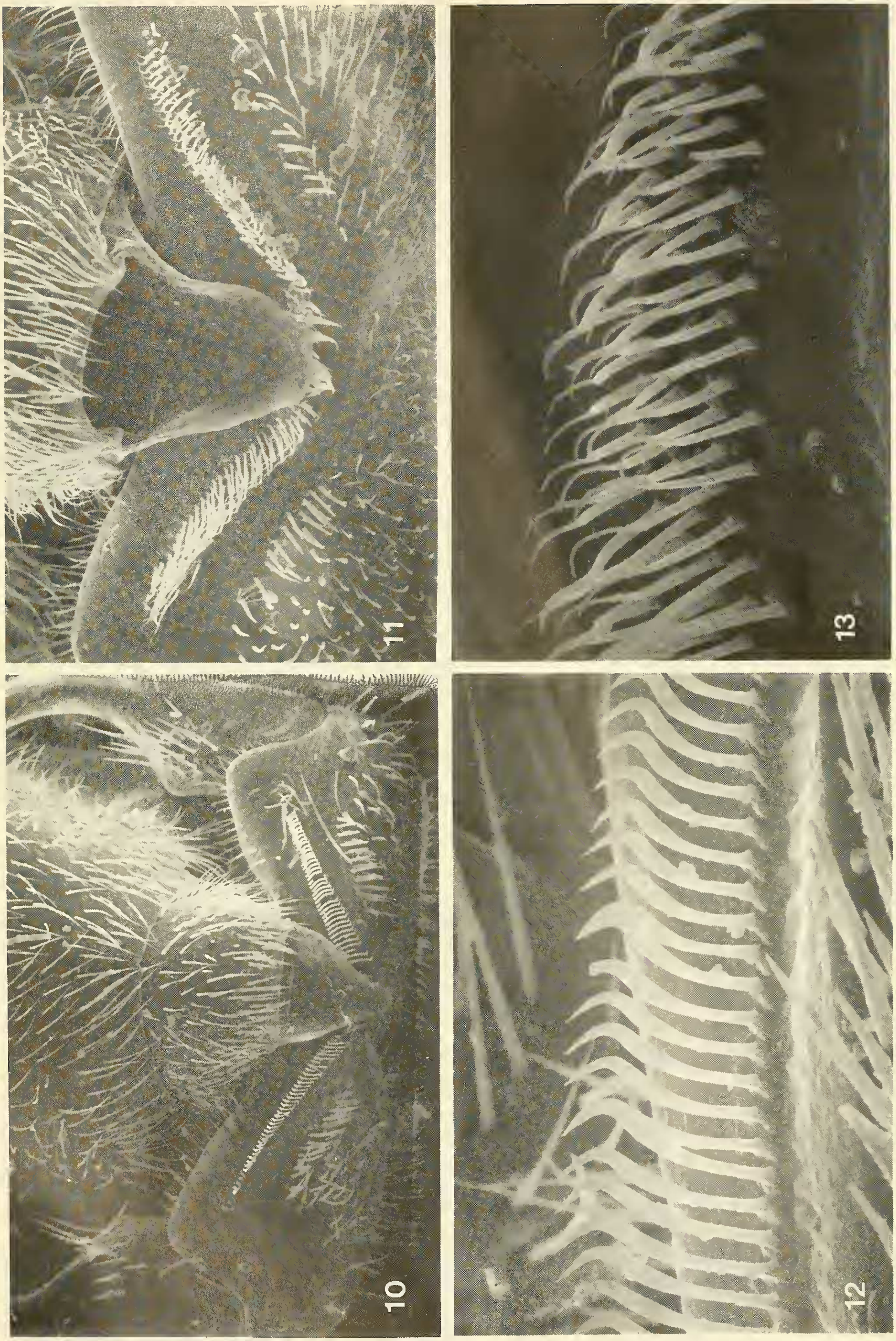


Fig. 9. Cladogram of *Limnonabis* species based on table 2. Nodes denoted by letters in circles. Characters and character states of synapomorphies given under each node.



Figs. 10-11. Posterior view of male genital capsule showing Ekblom's organ. 10. N. *americolimbata*, single row of spines. 11. N. *propinqua*, multiple rows of spines. Figs. 12-13. Structure of individual spines of Ekblom's organ. 12. N. *americolimbata*. 13. N. *propinqua*.

Table 2. Description of characters used in the cladistic analysis of the subgenus *Limnonabis*. Character states are preceeded by their coding in the data matrix and (in parentheses) the number of times state arises in the cladogram.

Female Genitalia
1. 0(1) Double sclerotized ring.
   1(1) Single sclerotized rings.
2. 0(1) Sclerotized ring symmetric, located medio-dorsal.
   1(1) Sclerotized ring asymmetric, located laterally.
3. 0(1) Membranous "sac" around sclerotized ring absent.
   1(1) Membranous "sac" symmetric, located dorsally.
   2(1) Membranous "sac" asymmetric, not located dorsally.
4. 0(1) Muscular "lobe" antero-ventral to sperm ducts absent.
   1(1) Muscular "lobe" antero-ventral to sperm ducts present.

Male Aedeagus
5. 0(1) Aedeagus with fewer than three sclerites.
   1(1) Aedeagus with 3 sclerites.
   2(1) Aedeagus with 4 sclerites.
   3(1) Aedeagus with more than 4 sclerites.
6. 0(1) Length of sclerite I less than four times its width at middle.
   1(1) Length of sclerite I at least four times its width.
7. 0(2) Sclerite I without flanges present.
   1(1) Sclerite I with flanges.
   2(1) Sclerite I with flanges only slightly developed.
8. 0(1) Sclerite II absent.
   1(1) Length of sclerite II less than three times its width.
   2(1) Length of sclerite II three times its width.
9. 0(1) Sclerite II without flanges.
   1(1) Sclerite II with flanges.
10. 0(1) Sclerite III linear without flanges.
   1(1) Sclerite III prong-shaped.
   2(1) Sclerite III comb-shaped.
   3(1) Sclerite III short, not linear.
   4(1) Sclerite III linear with flanges.
11. 0(1) Sclerite IV absent.
   1(1) Sclerite IV with recurved arm.
   2(1) Sclerite IV comb-shaped.

Male Paramere
12. 0(1) Tip of paramere not elongate.
   1(2) Tip of paramere elongate.
13. 0(1) Apex of paramere straight.
   1(2) Apex of paramere bent laterally.

External Structure and Form
14. 0(1) Head straight or converging behind eyes.
   1(1) Head diverging behind eyes.
15. 0(1) Medial half of male connexivum straight.
   1(1) Medial half of male connexivum curved under and appressed to abdomen.
16. 0(1) Spines of Ekblom's organ in a single linear row.
   1(1) Spines of Ekblom's organ in a bunched row.
17. 0(1) Body length less than 5 times the width.
   1(1) Body length greater than 5 times the width.

paramere (2 characters), aedeagus (6 characters), male genital capsule (1 character), female genitalia (3 characters), body structure (4 characters) (table 2). Determining the polarity of some of the characters was difficult, because the homology of some of the structures in other genera could not be determined and no previous cladistic analysis within the Nabidae was available for comparison. Because of these problems, we included the following three taxa in our analysis as outgroups, *Nabicula* (*Dolichonabis*) *limbata* (Dahlbom); *Nabicula* (*Nabicula*) *flavomarginata* (Scholtz); *Anaptus major* (A. Costa) (table 3). These taxa were chosen because they represent the other two subgenera of *Nabicula* and a more distant member of the tribe Nabini. All multistate characters were coded as ordered except characters 5 and 10 because we were uncertain of their transformation sequences.

The analysis produced a single tree of minimal length (31 steps, consistency index of 83.0, fig. 9). The subgenus *Limnonabis* appears to be a monophyletic group, as indicated by component E of the cladogram. It is identified by characters 14 and 15, the diverging posterior margin of the head, and the recurved connexivum of the male respectively. These are two of the characters Kerzhner (1968) used to define the subgenus. We are doubtful of the integrity of the first character, the diverging posterior lobe of the head. We have examined species in other genera (*Nabis* Latreille, *Lasiomerus* Reuter) in which this character displays almost the same development as seen in *Limnonabis*. At this time, we can find no genitalic characters that unite all species currently placed in *Limnonabis* and the only character that we feel defines the group is the recurved connexivum of the male.

The *ussuriensis* group does not appear to be a natural one, its members are united only by plesiomorphic characters, such as the single row of spines of Ekblom's organ. *Nabicula ussuriensis* is actually united with the *lineata* group by the presence of an asymmetric sclerotized ring (2-1) (character-character state), presence of a membranous "sac" around sclerotized ring (3), aedeagus with four sclerites (5-2), length of sclerite II three times its width (8-2) and sclerite II with flanges (9-1) (component C). The *lineata* group of Kerzhner (1968) is clearly monophyletic, represented by component B on the cladogram and defined by the asymmetric membranous sac (3-2), muscular lobe

Table 3. Character matrix for *Limnonabis* processed by HENNIG86.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Anaptus	1	0	0	0	3	0	0	?	0	?	?	1	0	0	0	0	0
flavomarginata	0	0	0	0	0	1	0	?	?	?	0	1	0	0	0	0	0
limbata	1	0	0	0	0	1	1	?	?	?	0	1	0	0	0	0	0
sauteri	1	0	0	?	1	1	1	0	0	3	0	0	0	1	1	0	0
demisa	1	0	0	0	1	0	0	1	0	1	0	0	1	1	1	0	1
usseriensis	1	1	1	0	2	1	1	2	1	4	2	0	1	1	1	0	1
propinqua	1	1	2	1	2	1	2	2	1	2	1	0	0	1	1	1	1
lineata	1	1	2	1	2	1	0	2	1	0	1	1	0	1	1	1	1
pontica	1	1	2	1	2	1	0	2	1	0	1	0	0	1	1	1	1

behind the sperm ducts (4-1), and the bunched row of spines comprising the Ekblom's organ (16-1). The latter character appears to be unique among the Nabidae. *Nabicula propinqua*, *N. lineata*, and *N. pontica* display a bunched row, 3-5 spines wide, on each side of the anal tube (fig. 11). All other species of nabids that we have examined possess only a single row of linearly arranged spines (fig. 10). The structure of the individual spines may also prove to be an informative character. In *N. propinqua*, the spines are thin, with the distal third sharply narrowed, sinuous, with the apex curved laterally (fig. 13), while in *N.* (*Limnonabis*) *americolimbata* the spines are wider, with the distal halves flattened and expanded (fig. 12).

Nabicula lineata and *N. pontica* are united by having sclerite III linear and without flanges (10-0) and sclerite I without flanges (7-0). This latter character is homoplasious, because the 0 state also appears in *N. demisa*.

Biogeography

All members of the subgenus *Limnonabis*, with the exception of *Nabicula propinqua*, are found in the Palaearctic region. The three species arising

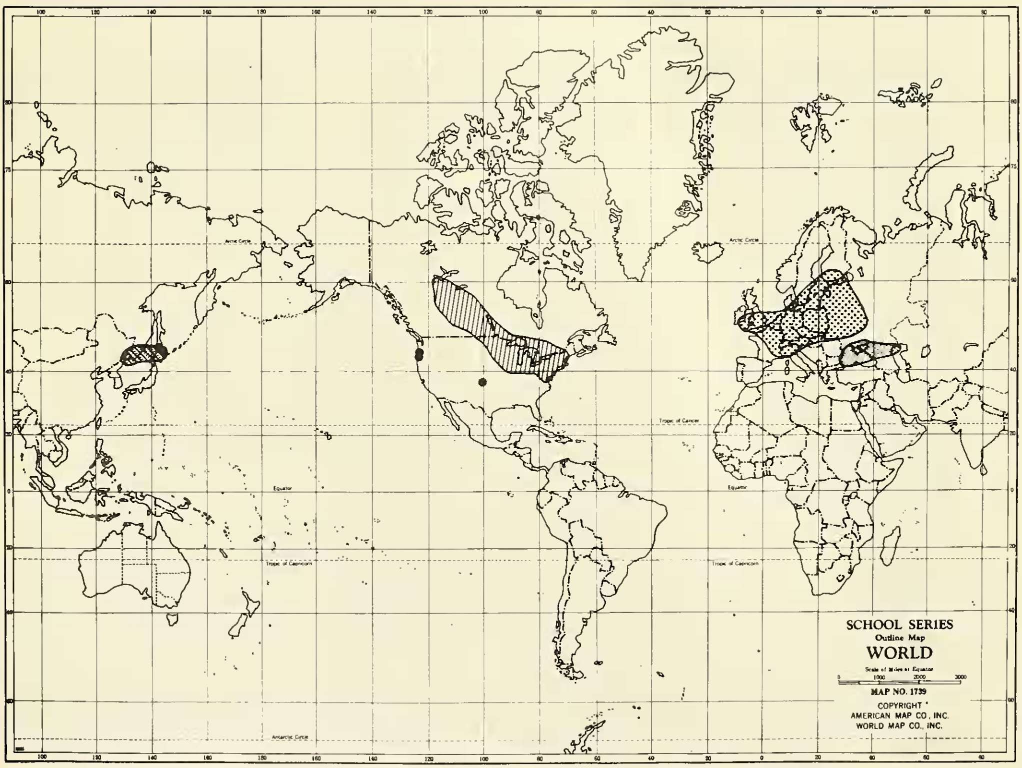


Fig. 14. Distribution of the subgenus *Limnonabis*. Vertical lines and solid circles in North America, *N. propinqua*. Large dots in Europe, *N. lineata*. Small dots in southeastern Europe, *N. pontica*. Slanted lines with small dots in southeast Asia, composite ranges of *N. ussuriensis*, *N. demisa* and *N. sauteri*.

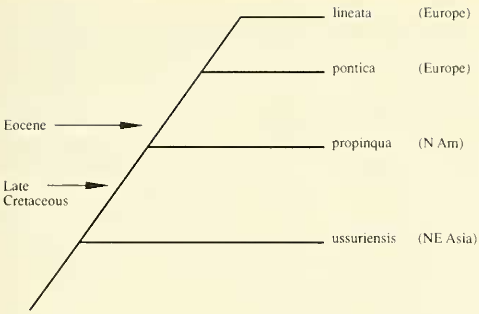


Fig. 15. Cladogram of *Limnonabis* with the present distribution indicated after each species name. Hypothesized ages of intercontinental vicariances indicated at left.

from the cladogram first, *N. ussuriensis*, *N. demisa* and *N. sauteri* occur in far eastern Asia (fig. 14). Two members of the *lineata* group, *N. lineata* and *N. pontica* occur in Europe and the Mediterranean region and *N. propinqua* occurs only in North America. With regard to the views of Ball (1975), we generated a testable biogeographic hypothesis to explain the present distribution of the members of the monophyletic group represented by component C on the cladogram. We chose to use only this group and not all of *Limnonabis*, because *N. sauteri* and *N. demisa* are primitive taxa whose placement in the subgenus appears tenuous.

We hypothesize that the distributions of the species in component C are the result of vicariance caused by the breakup of Laurasia beginning in the Cretaceous. With the development of the Turgai straits in the late Cretaceous, Asiamerica and Euramerica were separated into two distinct land masses (Cox 1974). This would have resulted in the ancestral population being divided into two groups, with the ancestor of *N. ussuriensis* in western Asiamerica and the ancestors of the *lineata* group in Euramerica.

The ancestor of the *lineata* group was distributed throughout Euramerica and with the opening of the North Atlantic eventually separating North America from Europe in the Eocene, the ancestor of *N. propinqua* was isolated from that of *N. lineata* and *N. pontica*. The exact time of separation of these two groups cannot be known because there were several distinct land bridges that closed at different times, with at least one dispersal route across the Thulean bridge which may have persisted into the Miocene 20 millions years ago (Noonan 1988). With the exception of the elongate apex of the paramere in *N. lineata*, *N. lineata* and *N. pontica* are very similar, suggesting that the separation of these two species is a more recent event.

In summary, we invoke two vicariant events to explain the origin and present distribution of the taxa in component C of the cladogram (fig. 15). 1) The ancestor of *N. ussuriensis* was isolated in Asiamerica from component B in Euramerica by the Turgai Straits. 2) The ancestor of *N. propinqua* was isolated from component A in Europe by the opening of the Atlantic. If our phylogenetic hypothesis is correct, we believe this biogeographic scenario to be the most parsimonious one. A dispersal hypothesis for the evolution of component C would require the ancestral form to have moved into, and then gone extinct from an area reaching from Eastern Europe to Eastern Asia. Likewise, dispersal of the ancestor of *N. propinqua* from Europe to North America via Beringia as suggested by Schaefer & Calabrese (1980), would require the extinction of this taxon in all of northern Asia. Another hypothesis for *propinqua* reaching North America is by dispersal across the North Atlantic. Because of the specialized habits, low incidence of macroptery and low vagility of this species (it has not been recorded from flight traps or aerial sampling), we consider the latter hypothesis unlikely.

Discussion

Using examples from the Trichoptera, Homoptera and Coleoptera, Allen (1983) discussed the North America – Europe – Northeast Asia distributions for insects. He found a common pattern among these groups in which the North American and European taxa shared a common ancestor after the origin of the Northeast Asian groups. Similar to our hypothesis for *Limnonabis*, Platnick (1976) discussed the vicariant patterns in the spider genus *Callilepis* (Gnaphosidae). His phylogenetic analysis of the genus showed that species groups were distributed in areas that reflected the breakup of Laurasia. He also suggested that the Turgai straights separated a Asiamerica group from a Euramerica one, and the Atlantic rift further separated the Euramerica group.

The species in the *N. lineata* group are very similar morphologically, differing primarily in the structure of the internal genitalia. It may seem unusual that we invoke such great ages for the separation of these species in light of the slight degree of morphological divergence. Without rehashing the old and continuing debate regarding rates of evolution, we feel that our hypothesis is tenable for three reasons. First, with few exceptions (e.g. *Nabicula subcoleoptrata* Kirby) the lineages within the tribe Nabini appear to be highly conservative or canalized in their morphology. Many species differ only slightly in external morphology and are distinguished primarily by the male aedeagus and the seminal depository of the female.

Second, explosive speciation and morphological evolution is often correlated with changing envi-

ronments or lineages radiating into new adaptive landscapes (Simpson 1944), while groups occupying stable, constant and predictable environments may undergo very little change through time. The *lineata* group inhabits moist, marshy habitats and secondarily, estuarine marshes, environments that prevailed during the Cenozoic but also have persisted relatively unchanged to the present. Considering the stability of morphology in the group, low vagility and their specific, unchanged habitat, large scale vicariant events resulting in superficially similar, disjunct species might be expected.

Finally, it is becoming increasingly apparent that in some groups of insects, extant species are of great antiquity. In the Coleoptera for example, the Pleistocene climatic oscillations greatly altered distributions but did not result in speciation (Coope 1970, Matthews 1977). Some species of beetles are apparently in excess of 10 million years old (Larsson 1978). Similar examples are available for the Heteroptera, (Calabrese 1978, 1980).

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APPENDIX

Literature Records

Canada. -- Alberta: Edmonton (Strickland 1953).

United States. -- Illinois: Cook Co.: Argo; West Pullman (Blatchley 1926). – Iowa: Hancock Co.: 8 mi. SE Britt, July 6, 1928 (Hendrickson 1930). – Maryland: Somerset Co.: Deal Island, June 29, 1970 (Froeschner 1970). – Michigan: Berrien Co.: New Buffalo & Stevensville (Hussey 1922b). – New Jersey: Morris Co.: Snake Hill; ?? Co.: White's Bay, July 20, 1914 (Froeschner 1971). – North Dakota: Ramsey Co.: Devils Lake, July 22 & 25 (Hussey 1922a). – South Dakota: Day Co.: Waubay, August 21, 1924 (Harris 1943); Grant Co.: Bigstone, August 20, 1924 (Harris 1943).

Specimens Examined

Canada. — Alberta: High Prairie, July 17, 1961, A. R. Brooks, 1 ♂, 1 ♀ (OSU); Slave Lake, August 14, 1924, O. Bryant, 2 ♂, 1 ♀ (CAS). – Manitoba: Red Deer R., August 3, 1937, C. L. Johnston, 1 ♂ (KU); The Pas, August 11, 1937, D. G. Denning, 1 ♀ (UM). – North West Territory: 5 mi. SE Ft. Providence, August 15, 1965, J. & W. Ivie, 1 ♀ (AMNH). – Ontario: Thessolon Lake, shore, July 21, 1965, J. & W. Ivie, 1 ♀ (AMNH). – Quebec: Quinze Lake, August 15, 1907, W. J. Palmer, 1 ♀ (CAS); Saskatchewan: Qu' Appelle River, N Tuxford, July 29, 1965, J. & W. Ivie, 2 ♀ (AMNH).

United States. — Illinois: Boone Co.: Belvidere, June 27, 1955, J.A. Slater (OSU); Fulton Co.: Havana, June 9, 1905 / Ill. Sands, Hart Coll. / *Nabis elongatus* Hart, type / *Reduviolus elongatus* Hart / TYPE *Nabis elongatus*, C. A. Hart, 1 ♂ (INHS); Lake Co.: Fox Lake, August 23, 1944, Frison & Ross, 4 ♂, 9 ♀ (INHS); Lake Villa, swamp, August 10, 1906 / *Reduvolius vicarius* Reuter, micr. F / *Nabis propinquus* Reuter, H. M. Harris / Van Duzee Cat. No. 825 Det. Harris, 1 ♀ (INHS); Waukegan, May 14, 1930 4 ♂ (INHS); Waukegan, beach, August 23, 1906 / *Reduvolius vicarius* Reut., Micro. M / *Nabis propinquus* Reuter, Det. H. M. Harris / Van Duzee Cat. No. 825, Det. Harris 1 ♂, 1 nymph (INHS). – Kansas: Meade Co.: September 13, 1944, R. H. Beamer, 1 ♂ (OSU). – Maine: Sagadahoc Co.: Popham Beach, September 4, 1920, A. P. Morse, 1 ♀, (AMNH). – Massachusetts: Essex Co.: Beach Bluff, 22 June, 1914, H. M. Parshley, 1 nymph (CAS); 13 August, 1914, ex. *Carex*, 2 ♂, 4 ♀; June 21, 1915, 1 nymph (CAS); August 17, 1916, ex. *Carex*, 3 ♂, 11 ♀ (AMNH); Middlesex Co.: Faneuil, August 2, 1904, A. P. Morse, 1 ♂; August 12, 1904, A. P. Morse, 1 ♀; October 1, 1904, A. P. Morse, 1 ♀ (AMNH). – Michigan: Cheboygan Co.: July 25, 1940, L. Spencer, 1 ♀ (OSU); July 1, 1950 J. D. Lattin, 1 nymph (OSU); Duncan Bay, July 27, 1957, W. J. Hangan, 2 ♀ (KU); Emmet Co.: August 10, 1950, J. D. Lattin, 1 ♀ (OSU); Huron Co.: Sand Point, June 24, 1922, R. ♀. Hussey, 1 ♀ (FSCA). – Minnesota: Saint Louis Co.: Eaglesnest, July 15, 1959, W. V. Balduf, 2 ♂, 1 ♀ (UM); Traverse Co.: Lake Traverse, 7.5 mi SW Wheaton, July 27, 1974, B. Tollefson, 1 ♂, 1 ♀ (UCB). – New York: Cattaraugus Co.: South Dayton, 23 July, 1946, R. H. Beamer, 1 ♀ (KU); Erie Co.: Buffalo, July 16, 1901, 1 ♀ (CAS); Nassau Co.: Long Island, Cold Spring Harbor Biol. Lab., B. Darnall, 1 ♀ (CAS); Piermont, June 17, 1934, Scholt, 1 ♀ (AMNH). – North Dakota: Ramsey Co.: Devil's Lake, July 22, 1920, T. H. Hubbell, 1 ♂ (FSCA). – Ohio: Erie Co.: Cedar Point, Sandusky, August 31, 1905, Van Duzee, 1 ♀ (UCB); Union Co.??, Camp Perry, September 5, 1921, W. L. McAtee, 1 ♀ (USNM). – Oregon: Coos Co.:

South Slough Sanctuary, SW Coos Bay, September 24. 1988, A. Asquith, 1 ♀ (OSU); Tillamook Co.: Island Camp, near woods, July 18, 1959, K. Fender, 1 ♂ (OSU); 5 mi E Pacific City, meadow, September 9, 1962, J. Capizzi, 2 ♀ (OSU); Sand Beach St. Pk., Sand Lake, September 7, 1988, A. Asquith & J. D. Lattin, 4 ♂, 12 ♀ (OSU). – Wisconsin: Dane Co.: T6N, RTE, S28, stream edge, aquatic net, September 14, 1973, J. Hender, 1 ♀ (UWiM); Wood Co.?, Nevin Marsh, July 23, 1974, site 6, sweep net, D. Bach, 1 ♂ (UWiM); July 11, 1974, site 2, D. Bach, 1 ♂ (UWiM).